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Effects of Photoperiod and Temperature on Growth, Flowering and Fruit Yield in Annual-Fruiting Red Raspberry Cultivars (*Rubus idaeus* L.)

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Summary

Plants of the annual-fruiting raspberry (*Rubus idaeus* L.) cultivars 'Autumn Treasure', 'Erika' and 'Polka' were raised in a phytotron under different temperature and day-length conditions for six weeks, and subsequently cropped in an open plastic tunnel at latitude 61°N. Flowering and fruit maturation were advanced and yield increased with increasing raising temperature over the 15–25 °C range in 'Erika' and 'Polka', while 20 °C was optimal for 'Autumn Treasure'. Long day (LD) conditions (20 h) likewise advanced flowering and increased fruit yield compared with 10 h photoperiod at all temperatures in 'Erika' and 'Polka', while photoperiod had no significant effect on flowering and fruit yield in 'Autumn Treasure'. In agreement with earlier findings, low temperature vernalization at 6 °C for six weeks increased flowering and fruit yield in 'Polka' compared with control plants raised at 18 °C. Vernalization also advanced the transition to flowering by reducing the number of nodes formed before flowering in 'Autumn Treasure' without increasing fruit yield, while flowering and fruiting were not promoted by vernalization in 'Erika'. 'Erika' out-yielded the other cultivars under all conditions and produced remarkable yields of 3.3 kg plant^{-1} when raised in LD at 25 °C. With its great yield potential and large fruits with excellent flavour, 'Erika' presents itself as a very promising cultivar, especially for environments with long growing season. The number of fruiting nodes was the single most important plant structural component associated with high fruit yield, accounting for 76 % of the total variation in the total data material.

Key words. flowering – fruit yield – photoperiod – plant architecture – raspberry – temperature – vernalization

Introduction

While the environmental control of growth and flowering in the traditional biennial-fruiting red raspberry cultivars (*Rubus idaeus* L.) have been quite extensively studied, much less is known about the environmental responses of their annual-fruiting counterparts. The subject was recently reviewed by Heide and Sønsteby (2011), and the contrasting flowering and dormancy regulation mechanisms of the two groups of cultivars were high-lighted. While biennial-fruiting cultivars have an absolute requirement for temperatures ≤ 15 °C for flower formation (Williams 1960; Sønsteby and Heide 2008), annual-fruiting cultivars readily initiate floral primordia at temperatures as high as 30 °C (Sønsteby and Heide 2009). Furthermore, while biennial-fruiting raspberry cultivars are facultative short day (SD) plants (Williams 1960; Sønsteby and Heide 2008), flowering is promoted by long days (LD) in at least some annual-fruiting cultivars (Sønsteby and Heide 2009). However, it remains to be established whether LD promotion of flowering is a common characteristic of annual-fruiting cultivars (see Heide and Sønsteby 2011).

While Carew et al. (2003) found no consistent effects of photoperiods ranging from 8 h to 17 h on growth rate in the cultivar 'Autumn Bliss', growth rate was consistently and significantly enhanced by long photoperiods (24 h) compared with 10 h photoperiods in the cultivar 'Polka' (Sønsteby and Heide 2009). However, since formation of new leaves was unaffected by photoperiod, this LD stimulation of shoot growth was due to increased internode length only. Similarly, while photoperiod had no significant effects on flowering time and abundance in 'Autumn Bliss' (Carew et al. 2003), flowering was consistently earlier and took place at lower nodes in 24-h than in 10-h photoperiods in the cultivar 'Polka' (Sønsteby and Heide 2009). Since night interruption (3 h light in the middle of a 14 h daily dark period) also significantly advanced flowering and reduced the number of leaves produced before flowering in the same way as day-length extension, it was concluded that this flowering response was a specific and genuine photoperiodic effect (Sønsteby and Heide 2009).

In addition to a general dormancy releasing effect of low temperature (chilling) on growth performance of shoots originating from root adventitious buds, chilling temperatures have also been found to have a distinct vernalization-like effect on flowering in annual fruiting raspberry. Thus, Carew et al. (2001) found that when young 'Autumn Bliss' plants produced from adequately chilled roots were exposed to additional chilling at 7 °C, the number of leaves produced before flowering decreased from 36 in non-chilled plants to 22 in plants chilled for 10 weeks. This was confirmed with 'Polka' plants produced from similarly chilled roots (Sønsteby and Heide 2009). When plants with five leaves were exposed to 6 °C for 7 weeks, both plant height and number of leaves before flowering decreased significantly compared with plants grown continuously at 24 °C. Although the time to anthesis did not decrease but tended to increase with extended chilling in both cultivars, it was concluded that in these annual fruiting cultivars there is a distinct vernalization-like advancement effect on flowering (Carew et al. 2001; Sønsteby and Heide 2009).

In order to study the interaction of temperature and photoperiod and to establish whether the reported advancements of flowering by LD and vernalization are representative for annual fruiting raspberry cultivars in general, we have compared the responses to such treatments in three cultivars with diverse pedigrees.

Materials and Methods

Plant material and cultivation

Plants of the cultivars 'Autumn Treasure', 'Erika' and 'Polka' were propagated from adventitious root buds in late March, as described by Sønsteby and Heide (2009). 'Polka' is a Polish cultivar derived from the well known British cultivar 'Autumn Bliss' (Keep 1988; Danek 2002), the Italian-bred 'Erika' is a selection from crosses between 'Autumn Bliss' and the biennial-fruiting 'Tulameen' (Pitsioudis et al. 2007), while 'Autumn Treasure' is a recent, spine-free cultivar from the East Malling breeding programme in UK (Keep 1988; Meiosis, Ltd., 2009), The root material used for propagation had previously been chilled at 2 °C for 10 weeks. After establishing for two weeks in 12 cm plastic pots at 20 °C in 10 h photoperiod, the plants had an average height of 8.5 cm and an average of 7.5 leaves. The plants were then (on 8 April) divided into two experiments and subjected to a range of conditions in the Ås phytotron as specified below.

In Experiment 1 (Photoperiod Expt.), plants of the three cultivars were exposed to temperatures of 15, 20, or 25 °C in 10 h and 20 h photoperiods for six weeks. During daytime (08.00 h–18.00 h) the plants were located in daylight compartments, while during the rest of the day, they were moved into adjacent growth rooms with darkness (10 h photoperiod) or low-intensity incandescent light (7 μmol quanta m^{-2} s^{-1}) for day-length extension to 20 h (18.00 h–04.00 h). Whenever the photosynthetic photon flux density (PPFD) in the daylight compartments fell below 150 μmol quanta m^{-2} s^{-1}, as on cloudy days, an additional 125 μmol quanta m^{-2} s^{-1} was automatically added using Philips HPT-I 400 W lamps. In Experiment 2 (Vernalization Expt.) plants of the same cultivars were subjected to temperatures of 6 °C and 18 °C for six weeks in two growth rooms with artificial light provided by Philips HPT-I 400 W lamps at a PPFD of 250 μmol m^{-2} s^{-1}, and a photoperiod of 10 h. In both experiments the temperatures were controlled to ±1 °C and a water vapour pressure deficit of 530 Pa was maintained at all temperatures.

After six weeks under the specified conditions (on 20 May), the plants were transplanted into 3 l plastic pots and transferred to an open Haygrove plastic tunnel at the Apelsvoll Experimental Station in the central part of South Norway (60° 40' N, 10° 52' E; 250 m altitude) for continued growth, flowering and fruiting. The temperature conditions in the tunnel during the growing season, as recorded every 30 min and stored on a temperature USB data-logger (EL-USB-2, Lascar electronics, UK), are shown in Fig. 1. At all stages of cultivation, the plants were grown in a coarse-textured sphagnum peat growth medium with a pH of 5.8. In the tunnel, the plants were placed in rows on a ground cover of black Mypex plastic with an inter-row spacing of 2 m, with four plants per running m within the rows. Only one shoot per pot was allowed to grow, with all additional shoots being removed by repeated pruning. The plants were supported by fixing to plastic-coated steel wire trellis and fertilised by daily fertigation with a complete fertilizer solution as described by Sønsteby et al. (2009). Plant protection was provided by biological control methods only.

Experimental design, data observation and analysis

The experiments were fully factorial, with a split-plot design, with temperatures as main plots and photoperiods and cultivars as sub-plots. Both experiments were replicated with three randomised blocks, each consisting of five plants of each cultivar in each treatment (i.e. a total of 15 plants per treatment). During the six-week pre-treatment period in the phytotron, growth was monitored by weekly measurements of plant height and counting of node numbers in each plant. At the end of this period, plants were examined and the number of plants with macroscopically visible floral buds recorded. In the tunnel, time of flowering, expressed as the first (terminal) open flower (anthesis), was recorded three times per week. Berries were harvested two-to-three times per week from week 27 (week 29 in Expt. II) to week 40, and the numbers and weights of berries were recorded. At the end of the harvest season, the numbers of flowers and unripe berries remaining on each plant were recorded, and the

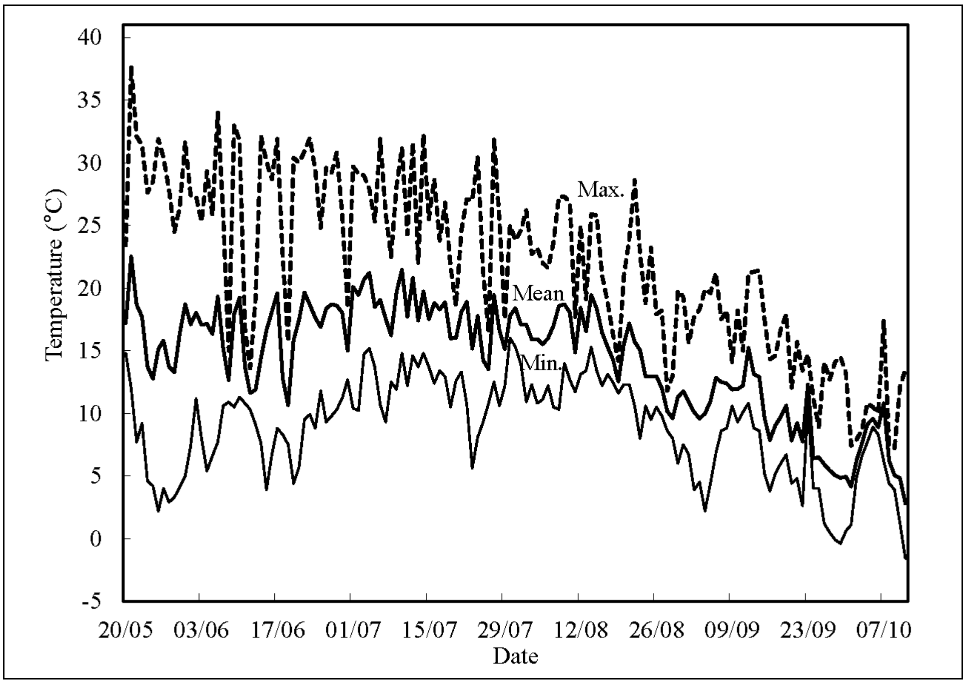

Fig. 1. Average daily mean, maximum and minimum temperatures as recorded in the plastic tunnel during the cropping period.

fruiting shoot architecture was registered by recording the final shoot height, number of dormant buds and fruiting laterals, as well as lateral length and the number of flowers and fruits on each lateral on all plants.

Data were subjected to analysis of variance (ANOVA) by standard procedures using a MiniTab® Statistical Software programme package (Release 15; Minitab Inc., State College, PA, USA). For analysis of the relationship between fruit yield and plant structure components, a stepwise regression analysis was also performed between yield data and plant architecture components, using the same software package. Percentage values were always subjected to arc sin transformation before the ANOVA.

Results

Photoperiod and temperature interactions (Experiment 1)

Shoot elongation growth during the six-week pre-treatment period increased consistently with increasing temperature and photoperiod (Fig. 2, Table 1), the effect of both factors being highly significant ($P < 0.001$). At the end of the six week period, there were also highly significant differences in final plant heights among the cultivars, 'Erika' having the tallest plants and 'Autumn Treasure' the smallest ones (Table 1). Since the relative effect of photoperiod decreased with increasing temperature, and since the cultivar difference varied somewhat with the temperature, there were also highly significant two-factor interactions of temperature × photoperiod and temperature × cultivar on plant heights (Fig. 2, Table 1). Initiation of new nodes also increased with increasing temperature and photoperiod (Fig. 2), the main effects of both factors being highly significant (Table 1). However, in 'Polka' and 'Erika', the photoperiodic effect varied among temperatures, so that in 'Polka' LD increased node numbers significantly at 15 °C only, in 'Erika' at 15 and 25 °C, but not at 20 °C. At this stage, the vigorous 'Erika' had the highest number of nodes under all temperature and day-length conditions (Fig. 2, Table 1).

Earliness of flowering varied significantly ($P < 0.001$) among the cultivars, but with different and sometimes contrasting responses to temperature and photoperiod (Table 1). Thus, at the end of the six week pre-treatment period, all 'Polka' plants in LD, and 60 % of those in SD, had visible flower buds at 25 °C; while only a small proportion of the 'Erika' plants had visible flower buds under these conditions, and on the other hand, none of the 'Autumn Treasure' plants had visible buds at this stage, regardless of temperature and day-length conditions. In both 'Polka' and 'Erika' the appearance of flower buds were markedly advanced by increasing temperature and photoperiod, effects that were also clearly expressed on time to first anthesis after transfer to the plastic tunnel (Table 2). 'Polka' started to flower approximately two weeks earlier than the other two cultivars and showed a gradual advancement of flowering with increasing temperature and photoperiod. However, in 'Autumn Treasure' and in some 'Erika' plants, the earliest flowering took place in plants which had been raised at 20 °C. The main effects of temperature, photoperiod and cultivar were all highly significant ($P < 0.005$) on both of these earliness parameters (Table 1, 2). Due to different temperature optima among the cultivars and a stronger temperature advancement of flowering in SD than in LD, there were

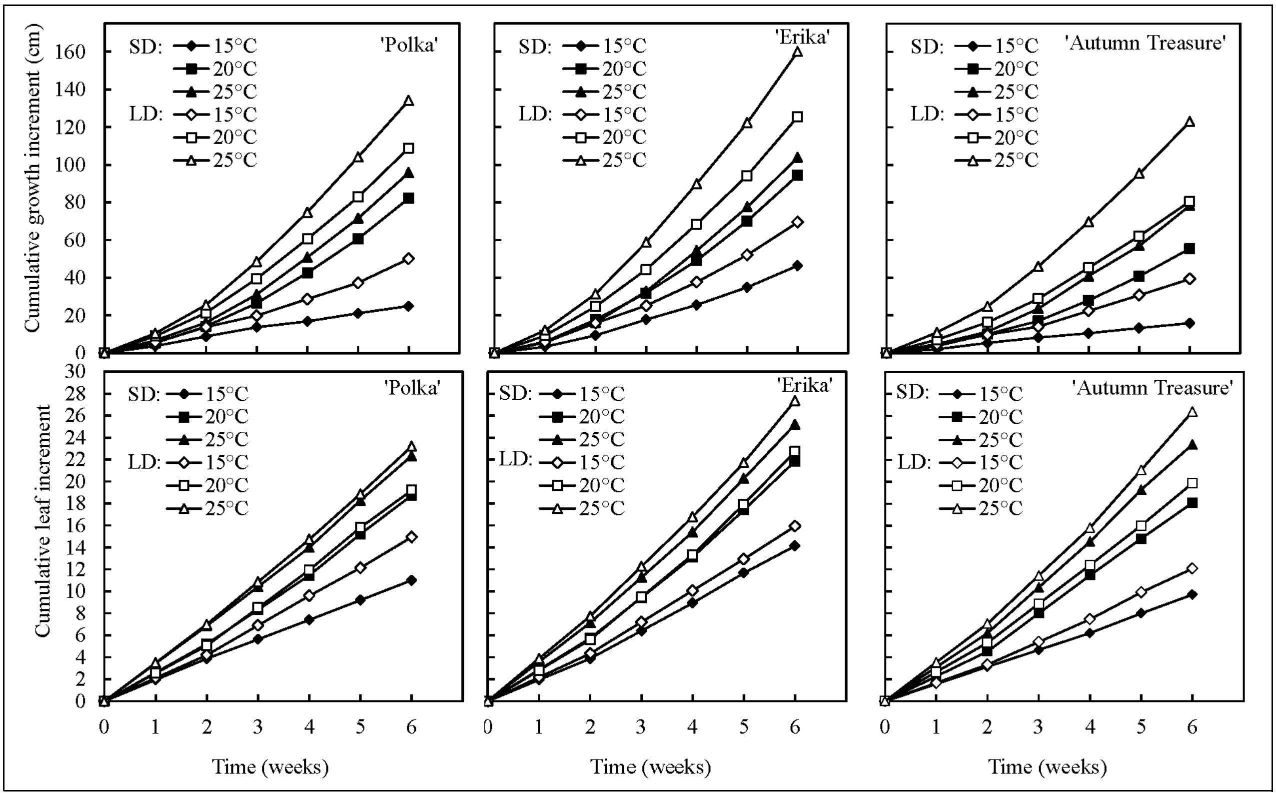

Fig. 2. Time courses of cumulative shoot growth and node formation under temperature and day-length conditions as indicated in three annual-fruiting raspberry cultivars. Each value is the mean of three replicates, each consisting of three plants. (n = 9).

also significant two-factor interactions of temperature × cultivar and temperature × photoperiod on these earliness parameters (Table 1, 2).

The early formation of flower buds in 'Polka' also resulted in early fruit ripening and rapid progress to fruit harvest, while delayed flowering in the other cultivars was associated with a parallel delay in harvest time (Table 2). However, the abundant flowering of 'Erika', also resulted in a long harvest period which lasted until fruit maturation was terminated by low temperature in October (Fig. 3). While the total harvested fruit yields increased with increasing temperature in the cultivars 'Polka' and 'Erika', the highest yields were obtained in plants raised at 20 °C in the cultivar 'Autumn Treasure'. Also, while fruit yields were higher in plants raised in LD in cultivars 'Polka' and 'Erika' (the only exception being 'Polka' at 15 °C), photoperiod had no significant effect on fruit yield in 'Autumn Treasure' (Table 2, Fig. 3). Both total yield and number of harvested fruits were more than twice as high in 'Erika' as in the other two cultivars which did not differ significantly in their yields (Fig. 3, Table 2). Fruit size varied highly significantly among the cultivars, averaging 7.0, 6.2 and 4.9 g across all temperature and photoperiod treatments in the cultivars 'Erika', 'Polka' and 'Autumn Treasure', respectively. Generally, fruit weight decreased with increasing temperature (Table 2), but since fruit weights also decreased with progress of the harvest period (data not shown), this effect was partially caused by the longer harvest periods in plants raised at high temperature. As previously observed (Sønsteby and Heide 2010), 'Autumn Treasure' had a tendency to produce fruits with split receptacles, resulting in fruits with branched tips.

While the early flowering and maturing 'Polka' managed to complete most of its crop before the harvest was terminated by low temperatures in early October, a large proportion of the great yield potential of the abundant-flowering and late maturing 'Erika' was not realized under the present conditions, particularly in plants raised in SD and low temperature (Table 2). Also 'Autumn Treasure' had a considerable number of flowers that did not reach to develop to mature fruits. In this cultivar, however, the number of such unrealized flowers was highest in plants raised in LD and high temperature. Because of the delayed flowering and fruiting in 'Autumn Treasure' plants raised at 25 °C, there were significant temperature × cultivar interactions on all parameters listed in Table 2.

Final shoot height, which is the combined result of inherent growth vigour and earliness of flowering, varied significantly among the cultivars, the vigorous 'Erika' being taller than the other two cultivars (Table 3). Final height increased with increasing temperature in 'Polka' and 'Autumn Treasure', while temperature had no significant effect on shoot height in 'Erika', apparently because

Table 1. Plant size and the percentage of plants with visible flower buds in three annual-fruiting raspberry cultivars after six weeks of raising at different temperature and day-length conditions in the phytotron.

Cultivar	Photoperiod (h)	Temperature (°C)	Shoot height (cm)	No. of nodes	Plants with flower buds (%)
'Polka'	10	15	24.9	11.0	0
		20	82.2	18.7	33
		25	95.8	22.3	60
	Mean		67.6 d⁺	17.4 cd	31 b
	20	15	50.1	14.9	0
		20	108.9	19.2	73
		25	134.1	23.2	100
	Mean		98.8 b	19.2 bc	59 a
'Erika'	10	15	46.4	14.1	0
		20	94.4	21.9	0
		25	103.9	25.2	7
	Mean		81.6 c	20.4 ab	2 c
	20	15	69.5	15.9	0
		20	125.5	22.7	7
		25	160.1	27.4	7
	Mean		117.4 a	21.9 a	5 bc
'Autumn Treasure'	10	15	15.9	9.7	0
		20	55.5	18.1	0
		25	78.3	23.4	0
	Mean		50.7 e	17.2 d	0 c
	20	15	39.3	12.1	0
		20	80.5	19.9	0
		25	122.9	26.4	0
	Mean		83.9 c	20.0 b	0 c
Probability levels of significance (ANOVA)					
Source of variation					
Temperature (A)			< 0.001	< 0.001	0.003
Photoperiod (B)			< 0.001	< 0.001	0.005
Cultivar (C)			< 0.001	< 0.001	< 0.001
A × B			< 0.001	NS	NS
A × C			0.002	0.03	< 0.001
B × C			NS	NS	0.002
A × B × C			NS	NS	NS

⁺ Mean values within the same column followed by different lower-case letters indicate a significant difference (P < 0.05) by Tukey's test. NS: Not significant.

delayed flowering at 15 °C in this cultivar resulted in a prolonged elongation period. Similarly, the final number of nodes, which is a measure of earliness of flowering in annual fruiting raspberries, varied significantly ($P < 0.001$) between the cultivars, being higher in the later-flowering 'Erika' and 'Autumn Treasure' than in the early-flowering 'Polka'. However, the cultivars exhibited different responses to photoperiod and temperature, the node number being significantly higher in SD than in LD in 'Polka', but with no significant response to photoperiod in 'Erika' and

Table 2. Effects of photoperiod and temperature during six weeks of raising on flowering and fruit yield components in three annual-fruiting raspberry cultivars.

Cultivar	Photo-period (h)	Tempera-ture (°C)	Days to first anthesis+	Days to 50 % harvest+	Harvested fruit yield (g plant^{-1})	No. of harvested fruits	Fruit weight (g)	Flowers and fruits not harvested	Total no of fruits and flowers
'Polka'	10	15	93.8	139.3	669.8	114.8	5.8	12.6	127.4
		20	78.3	127.7	854.9	119.0	7.1	3.3	122.3
		25	71.1	137.0	1591.3	273.5	5.8	24.2	297.6
	Mean		80.8 c++	134.7 c	1038.7 c	169.1 d	6.2 b	13.3 d	182.4 d
	20	15	84.7	133.7	600.1	97.3	6.2	11.3	108.5
		20	68.8	127.0	1104.9	168.3	6.6	12.8	181.1
		25	60.1	133.3	1846.4	326.9	5.7	34.8	361.7
	Mean		71.2 d	131.3 c	1183.8 c	197.5 d	6.1 b	19.6 d	217.1 cd
'Erika'	10	15	115.5	164.3	1770.5	229.8	7.7	415.1	644.9
		20	87.7	148.7	2830.9	403.3	7.0	280.7	684.1
		25	87.7	143.3	2727.3	436.7	6.2	204.5	641.2
	Mean		97.0 a	152.1 a	2442.9 b	356.6 b	7.0 a	300.1 a	656.7 a
	20	15	98.2	156.0	2751.6	368.5	7.5	320.5	689.1
		20	79.5	147.7	3144.2	445.4	7.1	159.6	605.0
		25	81.4	145.3	3360.0	532.5	6.3	234.1	766.6
	Mean		86.5 bc	149.7 ab	3085.3 a	448.8 a	6.9 a	238.1 b	686.9 a
'Autumn Treasure'	10	15	99.2	146.7	836.7	163.4	5.1	71.9	235.3
		20	93.7	143.0	1576.6	296.9	5.3	72.8	369.7
		25	95.9	145.0	1365.2	286.8	4.8	61.5	348.3
	Mean		96.1 a	144.9 b	1259.5 c	249.0 cd	5.1 c	68.7 cd	317.8 bc
	20	15	97.2	147.0	713.5	152.5	4.6	56.0	208.5
		20	87.3	141.3	1641.1	372.8	4.6	81.2	454.0
		25	96.4	145.0	1386.8	329.7	4.2	92.3	422.1
	Mean		93.5 ab	144.4 b	1247.1 c	285.0 bc	4.5 c	76.5 c	361.5 b
Probability levels of significance (ANOVA)									
Source of variation									
Temperature (A)			< 0.001	0.008	0.004	0.001	NS	NS	0.02
Photoperiod (B)			< 0.001	0.02	0.008	0.003	NS	NS	n.s.
Cultivar (C)			< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
A × B			NS	NS	NS	NS	NS	NS	NS
A × C			0.003	< 0.001	0.04	0.01	0.02	< 0.001	0.002
B × C			0.05	NS	0.02	NS	NS	0.03	n.s.
A × B × C			NS	NS	NS	NS	NS	NS	n.s.

+ Days from transfer to the plastic tunnel.
++ Mean values within the same column followed by different lower-case letters indicate a significant difference ($P < 0.05$) by Tukey's test.
NS: Not significant.

'Autumn Treasure'. Also, while node numbers increased with increasing temperature over the whole 15–25 °C range in 'Autumn Treasure', a minimum usually occurred in 'Erika' plants raised at 20 °C, while in 'Polka', node numbers were essentially unaffected by temperature (Table 3). Furthermore, the percentage of flowering nodes was nearly 50 % higher in 'Erika' than in the other two cultivars, a feature that contributed significantly to the high flower-

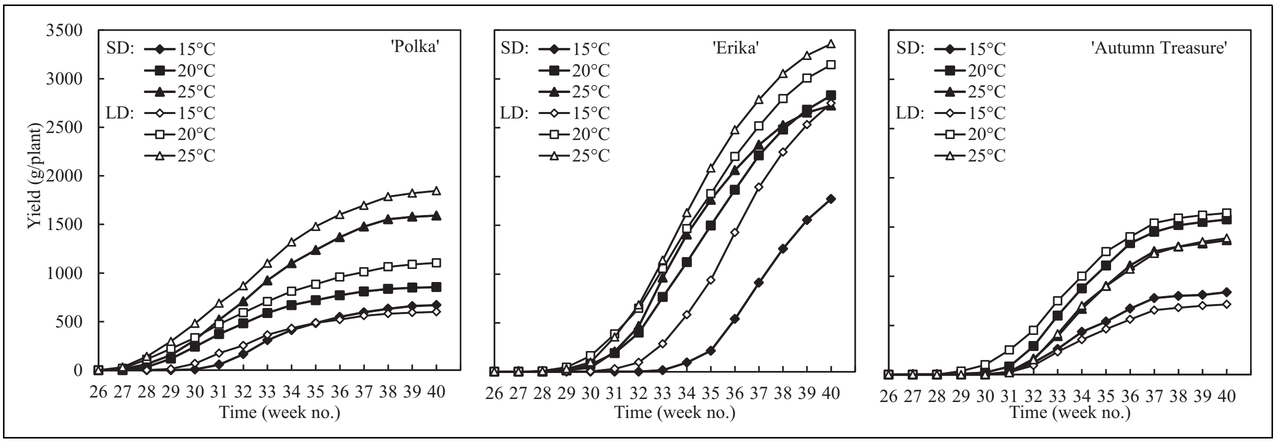

Fig. 3. Time courses of cumulative fruit yield in three annual-fruiting raspberry cultivars after raising for six weeks at the temperature and day-length conditions indicated. Each datum point represents the weekly mean harvest in g plant^{-1} for three replicates with three plants each.

ing and yield potential of this cultivar (Fig. 4). Thus, a stepwise regression analysis of fruit yield vs. the various plant architectural components identified the number of fruiting nodes as the single most important plant structural component associated with high fruit yield in the total data material, accounting for 76 % of the total variation ($R^2 = 0.68$; $P < 0.001$, N = 107). This component was followed in decreasing order of significance by the components 'Flowers per lateral' and 'Lateral length'. Jointly, these three components accounted for 91 % of the total yield variation. Although the temperature contribution to these responses varied somewhat between the cultivars, yielding a highly significant ($P = 0.002$) temperature × cultivar interaction, the proportion of flowering nodes generally increased with increasing temperature and photoperiod, the main effects being significant at P = 0.05 and 0.01, respectively (Table 3). The high flowering and yield potential of 'Erika' was further heightened by significantly longer fruiting laterals and more flowers per lateral in this cultivar than in the others (Table 3).

Effects of vernalization (Experiment 2)

Vernalization at 6 °C for six weeks in 10-h SD strongly restricted elongation growth and initiation of nodes compared with growth at 18 °C, although the cultivars varied significantly in their growth responses to temperature (Table 4). This resulted in a highly significant interaction of cultivar × temperature on elongation growth, while there was no parallel cultivar × temperature interaction on node numbers. At the end of the six-week treatment period, three 'Polka' plants out of 15 (20 %) had visible flower buds at 18 °C, while none were visible in the other cultivars or treatments (Table 4).

Flowering and yield performance of the plants after transfer to the plastic tunnel was also strongly influenced by the vernalization treatments, although with contrasting responses among the cultivars. While flowering (first anthesis) and fruit harvest were advanced by the 18 °C treatment in 'Polka' and 'Erika', high temperature tended to delay flowering and fruiting in 'Autumn Treasure', thus causing a highly significant ($P < 0.001$) temperature × cultivar interaction (Table 5). This interaction rendered the main earliness effect of temperature barely significant or, in the case of days to 50 % harvest, even non-significant. Harvested fruit yields were highly significantly affected by both temperature and cultivar, and again, with a highly significant temperature × cultivar interaction (Table 5). 'Erika' out-yielded the other cultivars under both temperature conditions, although in this cultivar and in 'Autumn Treasure' harvested yields were lower in the vernalized plants than in the control plants from 18 °C, while the opposite situation was found for 'Polka'. However, in the case of 'Erika', a large share of the crop did not reach maturity before harvest was terminated, and this was particularly the case with the vernalized plants. Thus, in these plants, less than a third of the initiated flowers reached maturity. With the addition of these flowers, the total number of fruits and flowers was not significantly different in the vernalized and the non-vernalized 'Erika' plants. Also in 'Polka' the number of unrealised flowers was higher in the vernalized plants, whereas in 'Autumn Treasure' both harvested crop and total number of flowers and fruits were higher in non-vernalized than in vernalized plants (Table 5). However, due to variation among replicates, none of these effects were statistically significant. Also, because of the contrasting cultivar responses, the main effect of temperature on total number of flowers and fruits was not significant in the ANOVA. As in the previous experiment, fruit weights varied significantly among the cultivars, 'Erika' having larger fruits than the others, while vernalization had no significant effect on fruit size.

The total number of nodes were significantly reduced by the vernalization treatment in cultivars 'Polka' and 'Autumn Treasure', indicating an advancement of the tran-

Table 3. Plant architectural characteristics of three annual-fruiting raspberry cultivars as influenced by photoperiod and temperature during a 6-week raising period.

Cultivar	Photoperiod (h)	Temperature (°C)	Final shoot height (cm)	Final number of nodes	Flowering nodes (%)	Mean lateral length (cm)	Fruit and flowers per lateral
'Polka'	10	15	122.8	34.0	35.7	21.6	10.4
		20	159.8	34.7	37.7	14.5	9.4
		25	149.0	33.8	51.6	30.0	17.1
	Mean		143.9 c+	34.2 b	41.7 b	22.0 c	12.3 c
	20	15	134.0	30.2	37.1	20.8	9.7
		20	157.2	29.7	41.5	16.9	15.0
		25	164.7	32.2	55.7	31.0	20.3
	Mean		151.9 c	30.7 c	44.7 b	22.9 c	15.0 bc
'Erika'	10	15	243.8	49.5	60.8	61.3	21.4
		20	200.8	42.2	65.5	59.4	24.5
		25	217.7	47.3	59.8	52.1	22.7
	Mean		220.8 a	46.3 a	62.0 a	57.6 a	22.9 a
	20	15	227.2	44.5	62.7	58.5	24.7
		20	218.7	39.7	64.8	61.0	23.9
		25	236.8	44.5	73.3	58.8	23.7
	Mean		227.6 a	42.9 a	66.9 a	59.5 a	24.0 a
'Autumn Treasure'	10	15	129.0	36.8	44.1	30.1	14.6
		20	165.8	44.7	43.0	29.1	16.8
		25	187.0	47.7	46.2	32.4	16.1
	Mean		160.6 c	43.1 a	44.4 b	30.5 b	15.8 bc
	20	15	155.3	39.0	42.3	28.1	12.7
		20	181.8	46.7	46.1	28.3	21.0
		25	207.5	49.3	46.7	30.1	18.4
	Mean		181.6 b	45.0 a	45.1 b	28.9 b	17.4 b
Probability levels of significance (ANOVA)							
Source of variation							
Temperature (A)			0.03	0.004	0.05	NS	0.02
Photoperiod (B)			0.005	0.03	0.01	NS	NS
Cultivar (C)			< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
A × B			NS	NS	NS	NS	NS
A × C			< 0.001	< 0.001	0.002	< 0.001	0.04
B × C			NS	0.03	NS	NS	NS
A × B × C			NS	NS	NS	NS	NS

Mean values within the same column followed by different lower-case letters indicate a significant difference ($P < 0.05$) by Tukey's test.
NS: Not significant.

sition to reproductive development (Table 6). Concurrent with this response, the percentage of flowering nodes was also significantly higher in the vernalized plants of these cultivars. In 'Erika' on the other hand, vernalization had no significant effect on any of these parameters, resulting in a highly significant temperature × cultivar interaction. However, because of the inherently high capacity for branching and flowering in 'Erika' (see Fig. 4), the average proportion of flowering nodes was almost as high in this cultivar, regardless of temperature treatments, as in vernalized plants of the other cultivars (Table 6). Furthermore, as in the previous experiment, mean lateral length

Fig. 4. Appearance of representative 'Erika' plant raised in LD at 20 °C. Note the long laterals and the extensive branching towards the base of the main shoot. Inserted above are fruiting branches of an 'Erika' plant raised in LD at 15 °C as it appeared on the last day of harvest, showing that a large number of flowers and fruits did not reach maturity. Both photos were taken on 10 October.

Table 4. Plant size and the percentage of plants with visible flower buds in three annual-fruiting raspberry cultivars after six weeks of vernalization at 6 °C or cultivation at 18 °C in 10 h photoperiod.

Cultivar	Temperature (°C)	Shoot height (cm)	No. of nodes	Plants with flower buds (%)
'Polka'	6	11.2 c+	11.4 cd	0
	18	72.4 a	21.6 ab	20
	Mean	41.8	16.5	10
'Erika'	6	18.5 c	13.0 c	0
	18	74.3 a	22.9 a	0
	Mean	46.4	18.0	0
'Autumn Treasure'	6	14.3 c	10.6 d	0
	18	55.1 b	19.7 b	0
	Mean	34.7	15.1	0
Probability levels of significance (ANOVA)				
Source of variation				
Temperature (A)		0.001	0.004	NS
Cultivar (B)		0.002	< 0.001	NS
A × B		0.005	NS	NS

+ Mean values within the same column followed by different lower-case letters indicate a significant difference (P < 0.05) by Tukey's test.
NS: Not significant.

and number of flowers per lateral were significantly higher in 'Erika' than in the other two cultivars.

Discussion

The results confirm our previous finding (Sønsteby and Heide 2009) that flowering in the annual fruiting raspberry cultivar 'Polka' is promoted and advanced by LD and low temperature vernalization during early stages of plant growth and development (Table 1, 5). The results also demonstrate that this early-induced advancement and increase of flowering was materialized into increased fruit yields as well. The results further demonstrate and confirm that apart from the vernalization effect, which was also demonstrated in the cultivar 'Autumn Bliss' by Carew et al. (2001), there is also a separate flower-promoting effect of relatively high temperature with optimum in the 20–25 °C range (see Heide and Sønsteby 2011). This temperature effect was enhanced by an interaction with LD (Table 2). As demonstrated by Sønsteby and Heide (2009), increased flowering and fruiting are associated with pronounced changes in plant architecture through marked increases in the proportion of flowering and fruiting *vs*. non-growing (dormant) buds. The same relations were observed in the present experiment (Table 3, 6).

The other cultivars varied, however, in their responses to photoperiod and temperature.

While flowering and fruiting were advanced and the yield enhanced in LD compared with SD also in 'Erika', photoperiod had no significant effect on these variables in 'Autumn Treasure' (Table 2). However, in the case of 'Erika' this yield increase was to some extent an earliness effect of LD, as a large share of the flowers initiated in SD did not reach maturity before harvest was terminated in the fall. This was particularly marked in plants raised at 15 °C. With the addition of these flowers, the total number of fruits and flowers were not significantly different in 'Erika' plants raised in LD or SD conditions (Table 2). In 'Autumn Treasure' on the other hand, the picture did not change with the addition of unrealized flowers.

Table 5. Effects of vernalization at 6 °C or cultivation at 18 °C for six weeks on flowering and fruit yield components in three annual-fruiting raspberry cultivars.

Cultivar	Temperature (°C)	Days to first anthesis+	Days to 50 % harvest+	Harvested fruit yield (g plant^{-1})	No. of harvested fruits	Fruit weight (g)	Flowers and fruits not harvested	Total no of fruits and flowers
'Polka'	6	92.4 b++	156.7 b	1030.9 b	200.9 ab	5.8 a	182.3 b	383.3 ab
	18	83.3 c	140.3 c	842.3 c	128.2 b	6.6 a	132.0 b	260.2 b
	Mean	87.7	148.5	936.6	164.6	6.2	157.2	321.7
'Erika'	6	102.4 a	164.3 a	1189.4 b	150.0 ab	7.9 a	554.2 a	704.2 a
	18	83.1 c	153.7 b	2175.7 a	287.7 a	7.6 a	310.0 b	597.7 ab
	Mean	90.3	159.0	1682.6	218.8	7.7	432.1	650.9
'Autumn Treasure'	6	90.3 bc	154.3 b	890.3 c	152.2 ab	5.9 a	142.7 b	294.9 b
	18	93.9 ab	158.3 ab	1145.5 b	193.1 ab	6.0 a	175.5 b	368.6 ab
	Mean	92.0	156.3	1018.9	172.7	5.9	159.1	331.7
Probability levels of significance (ANOVA)								
Source of variation								
Temperature (A)		0.03	NS	0.002	NS	NS	NS	NS
Cultivar (B)		0.01	< 0.001	< 0.001	NS	0.01	0.004	0.005
A × B		< 0.001	< 0.001	0.001	0.02	NS	NS	NS

+ Days from transfer to the plastic tunnel.
++ Mean values within the same column followed by different lower-case letters indicate a significant difference (P < 0.05) by Tukey's test.
NS: Not significant.

Since initiation of nodes is terminated by the formation of a terminal flower in annual-fruiting raspberry, the total number of nodes is a reliable physiological index of earliness of flowering that is independent of growth rate (Sønsteby and Heide 2009). Although the joint ANOVA for all cultivars presented in Table 3, revealed significant LD reduction in node numbers only in 'Polka' a separate ANOVA for each cultivar (data not shown) also revealed significant (P = 0.03) reductions in node number by LD in both 'Polka' and 'Erika', while the effect was non-significant in 'Autumn Treasure'. Therefore, on the basis of observations on earliness of flowering and fruit maturation, total flowering and fruit yield as well as the number of nodes formed before flowering, it can be concluded that LD significantly advanced and increased flowering and fruit yields in the cultivars 'Polka' and 'Erika', but not in 'Autumn Treasure' (Table 2). Based on the same criteria, and particularly in view of the large reduction of node numbers in vernalized plants of 'Polka' and 'Autumn Treasure' shown in Table 6, we likewise conclude that vernalization advanced the transition to flowering in 'Polka' and 'Autumn Treasure' but not in 'Erika'. At the same time, vernalization also nearly doubled the percentage of flowering nodes in the former cultivars. However, in 'Autumn Treasure' the advanced flowering was not associated with increased fruit yield (Table 5), possibly because of an early cessation of growth in the vernalized plants.

Also, while earliness and fruit yield generally increased with increasing raising temperature all the way up to 25 °C in 'Polka' and 'Erika', 'Autumn Treasure' had a consistent temperature optimum at 20 °C (Table 2, 3). This concurs with our earlier finding (Sønsteby and Heide 2010), that 'Autumn Treasure' deviates from other annual-fruiting raspberry cultivars studied so far by having a lower temperature optimum for floral initiation, the process being increasingly delayed at temperatures above 20 °C. These results reveal quite diverse photo-thermal flowering responses among annual-fruiting raspberry cultivars. This is in no way surprising, since species as diverse as *Rubus odoratus*, *R. spectabilis* and even *R. arcticus* have been introgressed into the gene-pool of the annual-fruiting raspberries (Keep 1988), thus creating a diverse and complex genetic background of these cultivars. It should also be remembered that 'Erika' originates from a cross between the annual-fruiting 'Autumn Bliss' and the biennial-fruiting cultivar 'Tulameen' (Pitsioudis et al. 2007).

Since flowering and yield increased with increasing temperature all the way up to 25 °C in 'Polka' and 'Erika', their optimal temperature could not be determined in Expt. 1. However, declining flowering at temperatures exceeding 25 °C in earlier experiments with the cultivars 'Autumn Bliss' and 'Polka' (Carew et al. 2003; Sønsteby and Heide 2009), suggests that the temperature optimum for all these cultivars is close to 25 °C.

Table 6. Plant architectural characteristics of three annual-fruiting raspberry cultivars as influenced by temperature (6 °C or 18 °C) during a 6-week raising period.

Cultivar	Temperature (°C)	Final shoot height (cm)	Total number of nodes	Flowering nodes (%)	Mean lateral length (cm)	Fruit and flowers per lateral
'Polka'	6	105.7 bc+	24.0 b	70.2 a	44.2 b	22.5 a
	18	149.2 abc	31.8 a	44.4 b	31.2	18.4 a
	Mean	127.4	27.9	57.3	37.7	20.4
'Erika'	6	190.5 a	37.3 a	67.5 a	53.3 ab	27.2 a
	18	169.2 a	36.0 a	65.5 a	61.3 a	25.5 a
	Mean	179.8	36.7	66.5	57.3	26.4
'Autumn Treasure'	6	90.2 c	24.2 b	71.2 a	42.7 b	17.5 a
	18	157.7 ab	38.3 a	44.8 b	43.3 b	21.5 a
	Mean	123.9	31.3	58.0	43.0	19.5
Probability levels of significance by ANOVA						
Source of variation						
Temperature (A)		0.05	0.005	0.02	NS	NS
Cultivar (B)		< 0.001	< 0.001	0.03	< 0.001	0.05
A × B		0.001	0.001	0.06	0.001	NS

+ Mean values within the same column followed by different lower-case letters indicate a significant difference (P < 0.05) by Tukey's test.
NS: Not significant.

The cultivar 'Erika' out-yielded the other cultivars by more than 100 % in Expt. 1 and approximately 80 % in Expt. 2. Plants raised in LD at 25 °C yielded remarkable 3.3 kg plant^{-1} of high-quality fruit, even though the full yield potential of the cultivar was not realized under the present conditions (Table 2, Fig. 4). Productivity of raspberries is mainly a function of the number of laterals produced per shoot, and the number and weights of fruits per lateral (Ourecky 1976; Keep 1988; Sønsteby et al. 2009; Sønsteby and Heide 2010). Therefore, the high yields of 'Erika' appeared to be expressed through the combined effects of vigorous growth resulting in large plants with many nodes, a positive balance of flowering *vs.* dormant nodes (few dormant buds), long and fruitful laterals, and large berries (Fig. 4). This was confirmed by the stepwise regression analysis which identified the number of fruiting nodes as the single most important plant structural component associated with high fruit yield in the total data material, accounting for 76 % of the total variation. As demonstrated by the data in Table 2 and 5, the environmental factors that contributed the most to this type of development were LD and relatively high temperature during early stages of plant growth in 'Polka' and 'Erika', and low temperature vernalization in 'Polka' and 'Autumn Treasure'. These results are in line with our earlier findings with these and other annual-fruiting cultivars (Sønsteby and Heide 2009; 2010).

Compared with the early flowering and maturing 'Polka' (cf. Sønsteby and Heide 2010), 'Erika' was relatively late and therefore, it did not realise its full yield potential under the present conditions. However, it should be kept in mind that it was this very lateness that to a large extent determined the cultivar's high yield potential as it allowed the building up of a large plant with many potential flowering laterals. Also, since flowering and fruit maturation in raspberries start at the top of the plant and spread sequentially to lower shoot positions (Sønsteby and Heide 2008), large plants with many laterals and abundant flowering, such as 'Erika', consequently will have a long harvest period.

Although 'Erika' clearly is too late for out-door production in the cool Nordic climate (Sønsteby and Heide 2010), it produced remarkable yields of more than 3 kg plant^{-1} in an open plastic tunnel after six-weeks of pre-culture under appropriate conditions (Table 2). This corresponds to more than 56 t ha^{-1} in our planting system. With its great yield potential and large berries with good flavour and firmness (Sønsteby and Heide 2010), 'Erika' presents itself as very promising for environments with longer growing seasons. However, for maintenance of satisfactory berry weights for the fresh market, coastal areas with relatively cool but long growing seasons would appear as the ideal environment for realization of the full potential of this promising cultivar.

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